INCIPIENT DRYING AND WILTING AS INDICATED BY MOVEMENTS OF COCONUT PINNAE [1]

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The amount of water in the plant at any time depends upon the relation between the rates of absorption and of transpiration that have recently been in operation. During the day most plants lose water more rapidly than they absorb it; in the night, on the other hand, plants usually absorb water more rapidly than they transpire it. Thus it is generally true that the water content of the plant is high in the night, especially after midnight, while it is lower during the day, especially in the afternoon; an incipient drying, or saturation deficit, of plant tissues generally appears early in the day and becomes progressively greater as the day advances. Incipient drying is accompanied by decreasing turgor in some or all of the leaf tissues and frequently results in actual wilting (Livingston and Brown, 7; Livingston, 6). This diurnal deficit appears to be one of the most important features in the complex relation of the plant to its water supply; and it has an important bearing on the general problems of drought resistance and irrigation of cultivated crops.

A method employed by Livingston and Brown (7) in studying the changes that occur in the relative water content of leaves throughout the day and night, is to gather a large number of similar leaves from hour to hour and to determine the moisture content of each lot as percentage of the dry or green weight. As pointed out by these workers, this method fails to take into account the small diurnal increase in materials other than water within the tissues; if the water content *per leaf* remained constant, such accumulation would of course *lower* the *percentage* of water on the basis of weight; but they regard the percentage changes shown by their data as mainly due to lowered water content per leaf, brought about when the ratio of the rate of water loss to that of water supply became less than unity. Similar results for the twigs of a desert plant were obtained by Edith B. Shreve (14).

Other workers (Lloyd, 10; Miller, 11) have employed circular leaf samples of known area, instead of entire leaves, and have calculated the water percentage on the basis of leaf area. The use of such samples makes it possible to study changes in weight that may be due to the accumulation of material other than water, but it does not permit a study of alterations due to changes in leaf area; according to Thoday (16), during wilting some kinds of leaves may shrink two or three or in some cases as much as six

percent.   A diminished water content in the plant as a whole has been studied also, by determining the difference between the rate of transpiration and that of absorption, as these rates vary independently throughout the day and night (Renner, 12, 13).

The present paper describes preliminary experiments that deal with what may offer another method, useful with some plants, for the indirect study of incipient drying; this method depends upon changes in leaf position or leaf shape, resulting from changes in leaf water content and concomitant alterations in the turgidity relations of different leaf tissues.

Leaves of the coconut (*Cocos nucifera*) were employed.   The leaf of this plant is primarily to be regarded as a very large, entire or merely notched leaf with very regular pinnately arranged veins reaching laterally outward from a central rib.   As it develops, the leaf blade tears, however, midway between each pair of adjacent veins, so that it comes to have the appearance of a pinnately compound leaf, the true midrib appearing like a rachis and the lateral veins appearing like the midribs of pinnae.   The lateral strips, separated by the tearing just mentioned, will be called pinnae in this paper.

It was noted by Copeland (2) that running ventrally for its entire length along each side of the midrib of the coconut pinna there is a narrow, colorless strip, the two strips together constituting a "hinge."   Through the action of the hinge the two wings of the pinna may take various positions, thus altering the general configuration of the pinna.   As Copeland has pointed out, when the leaves are well supplied with water the hinge cells are distended and the two pinna wings are held nearly in the same plane, like the right and left halves of an ordinary leaf; but when there is a deficiency of water in the hinge tissue the two pinna wings revolve downward, about the pinna midrib as an axis, so that their lower faces approach each other.   When the pinnae are on the point of beginning to curl on account of drying, the angle between the two wing faces is about 25 degrees of arc.   The total actual width of an average coconut pinna is about 3.5 cm., the wing width being half as great.   Since the two wings remain approximately flat until curling begins, simply moving upward or downward on the midrib as an axis, the angle between them may be conveniently approximated by means of the distance between the two free, parallel edges.   The behavior of the pinna hinges is illustrated by Copeland's (2) tables showing variations, for several days, in the distance between the edges of pinnae.

Since the action of the hinges and the resulting "opening" or "closing" of the pinnae appeared to be related to turgidity changes, it seemed desirable to study the movements with reference to the water content of the pinnae and to the temperature and evaporating power of the air.   The present paper reports a preliminary study of this kind.

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University of the Philippines, at Los Baños, during April and May, 1918, in connection with class work in plant physiology. It is a pleasure to acknowledge indebtedness to Prof. B. E. Livingston for suggestions in the preparation of this paper; and to members of the class, especially Mr. Pedro David and Mr. F. de Peralta, for assistance in securing the measurements.

<center>EXPERIMENTATION</center>

Excised pinna samples. To study the relation between water content and the degree of closure, pinnae were cut from a plant and taken to the laboratory, where the measurements were made. From near the middle of a pinna three 8-cm. lengths were cut. The pieces were weighed at intervals, the distance between the two free edges of each piece (here called its apparent width) being measured immediately after each weighing. After continuing the measurements for several hours, the area of one side of each piece was determined. They were then dried, and the water content was calculated for each weighing.

The results of five similar tests, made in the laboratory (temperature, 27° C.) with excised pieces of pinnae, are presented in table 1, three pieces being used in each test. From the average apparent width of the pinna in each case has been derived the average magnitude of the angle between the two lower faces of the pinna wings; and the average angular magnitudes are given, for the several observations, in the last column of the table; this value may be called the angle of pinna divergence, which is taken as related to the turgor condition of the two pinna hinges.
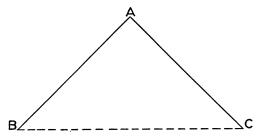

FIG. I.   Diagrammatic cross section of coconut pinna; lines AB and AC representing the two pinna wings, hinged to the midrib at A, and the line BC representing the apparent pinna width.

If the diagram of figure 1 represents a cross section of a coconut pinna, lines AB and AC representing the two pinna wings, hinged to the pinna midrib at A, then line BC represents the apparent pinna width for the cross section used. Determination of the average apparent width of the pinna sample used was made at each time of observation, and the apparent-width values are given in column 6 of the table. Determination of the average width of each of the two (similar) wings was also made for each

pinna sample, the value being taken to be constant for all observations. Returning to the diagram of figure 1, the quotient obtained by dividing half the length of line BC by the length of line AB (or by that of line AC, since these are equal) is the sine of half the angle BAC. From the sine is readily determined the magnitude of the half-angle itself (by use of a table of sine values), and multiplying this value by 2 gives the magnitude of the whole angle BAC, the angle of divergence of the two pinna wings. The last named magnitude, being the average for the pinna sample used, is the one given in the last column of the table, for each observation.

TABLE I.   *Relation between Water Content of Excised Portions of Pinnae and Average Angle of Divergence between the Two Pinna Wings*

Test No. and Values that Are Constant for the Test	Time Elapsed since Excision	Ave. Green Weight per 100 Sq. Cm. of Area (One Side)	Ave. Water Content per 100 Sq. Cm. of Area (One Side)		Ave. Apparent Width of Pinna Sample	Ave. Magnitude of Angular Divergence between Pinna Wings
			Actual (from Weight and Area of Samples)	Calculated from Equation of Smoothed Rectilinear Graph (see Discussion)		
Test I	*min.*	*grams*	*grams*	*grams*	*cm.*	*deg. of arc*
Ave. actual width of	0	4.7410	2.8938	2.8877	2.070	73° 30′
pinna wing, 1.73 cm. Ave.	5	4.7283	2.8811	2.8769	2.036	72° 6′
area of pinna sample (one	10	4.7165	2.8693	2.8686	2.010	71° 2′
side), 27.7 sq. cm. Ave.	15	4.7057	2.8585	2.8632	1.993	70° 20′
dry weight per 100 sq. cm.	20	4.6989	2.8517	2.8549	1.967	69° 18′
of area (one side), 1.8472 g.	25	4.6883	2.8411	2.8472	1.943	68° 20′
Equation constants (see	30	4.6818	2.8346	2.8335	1.900	66° 36′
discussion), $K = .3191$;	35	4.6753	2.8281	2.8303	1.890	66° 12′
$L = 2.2272$.	65	4.6267	2.7795	2.7824	1.740	60° 24′
	95	4.5733	2.7261	2.7208	1.547	53° 8′
	125	4.5187	2.6715	2.6685	1.383	47° 8′
	155	4.4619	2.6147	2.6155	1.217	41° 12′
	185	4.3982	2.5510	2.5485	1.007	33° 50′
	215	4.3414	2.4942	2.4994	0.853	28° 32′
Test II						
Ave. actual width of	0	4.1899	2.3759	2.3825	2.677	101° 22′
pinna wing, 1.73 cm. Ave.	30	4.1239	2.3099	2.3070	2.410	88° 18′
area of pinna sample (one	60	4.0711	2.2571	2.2570	2.233	80° 22′
side), 27.9 sq. cm. Ave.	90	4.0171	2.2031	2.2017	2.037	72° 8′
dry weight per 100 sq. cm.	120	3.9571	2.1431	2.1488	1.850	64° 40′
of area (one side), 1.8140 g.	150	3.8957	2.0817	2.0839	1.620	55° 50′
Equation constants (see						
discussion), $K = .2825$;						
$L = 1.6262$.						
Test III						
Ave. actual width of	0	4.0369	2.3144	2.3145	2.590	98° 52′
pinna wing, 1.71 cm. Ave.	30	3.9813	2.2588	2.2558	2.367	87° 56′
area of pinna sample (one	60	3.9330	2.2105	2.2164	2.217	81° 6′
side), 27.5 sq. cm. Ave.	90	3.8867	2.1642	2.1620	2.010	72° 14′
dry weight per 100 sq. cm.	120	3.8377	2.1152	2.1139	1.827	64° 48′
of area (one side), 1.7225 g.	150	3.7875	2.0650	2.0656	1.643	57° 38′
Equation constants (see						
discussion), $K = .2628$;						
$L = 1.6338$.						

TABLE I—*Continued*

Test No. and Values that Are Constant for the Test	Time Elapsed since Excision	Ave. Green Weight per 100 Sq. Cm. of Area (One Side)	Ave. Water Content per 100 Sq. Cm. of Area (One Side)		Ave. Apparent Width of Pinna Sample	Ave. Magnitude of Angular Divergence between Pinna Wings
			Actual (from Weight and Area of Samples)	Calculated from Equation of Smoothed Rectilinear Graph (see Discussion)		
	min.	*grams*	*grams*	*grams*	*cm.*	*deg. of arc*
Test IV	0	4.5473	2.7612	2.7558	1.683	65° 18′
Ave. actual width of pinna wing, 1.56 cm. Ave.	30	4.4870	2.7009	2.7074	1.543	59° 16′
area of pinna sample (one	60	4.4333	2.6472	2.6580	1.400	53° 20′
side), 24.9 sq. cm. Ave.	90	4.3837	2.5976	2.6106	1.263	47° 46′
dry weight per 100 sq. cm.	120	4.3363	2.5502	2.5681	1:140	42° 52′
of area (one side), 1.7861 g.	150	4.2834	2.4973	2.4920	0.920	34° 18′
Equation constants (see	180	4.2357	2.4496	2.4392	0.767	28° 28′
discussion), $K = .3457$; $L = 2.1740$.						
Test V	0	3.4292	1.9270	1.9268	1.890	69° 24′
Ave. actual width of pinna wing, 1.66 cm. Ave.	5	3.4186	1.9164	1.9153	1.823	66° 36′
area of pinna sample (one	10	3.4028	1.9006	1.9084	1.783	64° 58′
side), 26.6 sq. cm. Ave.	13	3.4023	1.9001	1.9038	1.756	63° 52′
dry weight per 100 sq. cm.	18	3.3915	1.8893	1.8912	1.683	60° 56′
of area (one side), 1.5022 g.	23	3.3785	1.8763	1.8787	1.610	58° 0′
Equation constants (see	28	3.3897	1.8675	1.8706	1.563	56° 10′
discussion), $K = .1718$;	30	3.3634	1.8612	1.8677	1.546	55° 30′
$L = 1.6021$.	36	3.3559	1.8537	1.8505	1.446	51° 38′
	43	3.3428	1.8406	1.8419	1.396	49° 44′
	47	3.3355	1.8333	1.8375	1.370	48° 44′
	50	3.3303	1.8281	1.8282	1.316	46° 42′
	58	3.3207	1.8185	1.8156	1.243	43° 58′
	64	3.3094	1.8072	1.8059	1.186	41° 52′

The equation constants given in column 1 and the calculated values of column 5 will be considered below.

Pinna still attached. For the study of angular changes in the pinnae still attached to the plant, ten pinnae were selected on each of three trees (thirty pinnae in all), and these were measured at hourly intervals, from 6 a.m. to 6 p.m., for six days. Ink marks on the pinna edges insured that the measurements would always be made at the same place. A shaded thermometer near the plants was read at the times of measurement, and a Livingston white spherical atmometer, unshaded and also near the plants, was likewise read.

The data thus secured are shown in table 2.

DISCUSSION OF RESULTS

Excised pinna samples. The results presented in table 1 show that excised pinnae in laboratory tests gradually lost weight as the result of transpiration unaccompanied by absorption, and that at the same time the

apparent pinna width gradually decreased. To study the relation between apparent pinna width and foliar water content, the apparent-width values (table 1, column 6) were plotted as abscissas of a graph and the average actual water contents (table 1, column 4) were plotted as ordinates. The five graphs obtained in this manner were all approximately straight lines, suggesting a linear relationship between the water content per unit of

TABLE 2. *Hourly Fluctuations in Apparent Pinna Width (for Pinnae Attached to the Plant), together with Hourly Temperature and Evaporation Data*

Time of Observation	Ave. Apparent Pinna Width (10 Pinnae on Each Plant)			Temperature	Evaporating Power of the Air (White Spherical Atmometer)
	Plant A	Plant B	Plant C		
	cm.	cm.	cm.	deg. C.	cc. per hr. for preceding hour
April 29					
6 a.m.	1.94	1.91	2.32	22	
7 a.m.	1.81	1.82	2.05	27	0.8
8 a.m.	1.76	1.73	1.97	29	1.6
9 a.m.	1.70	1.69	1.96	30	1.9
10 a.m.	1.59	1.68	1.87	31	1.7
11 a.m.	1.63	1.65	1.87	31	3.3
12 noon	1.56	1.68	1.80	33	3.6
1 p.m.	1.54	1.68	1.79	35	4.9
2 p.m.	1.50	1.50	1.97	37	4.4
3 p.m.	1.46	1.58	1.88	37	5.1
4 p.m.	1.65	1.57	1.86	34	3.6
5 p.m.	1.78	1.65	1.87	30	3.8
6 p.m.	1.87	1.75	1.90	28	1.4
April 30					
6 a.m.	1.96	1.96	2.26	23	
7 a.m.	1.84	1.83	2.00	28	0.9
8 a.m.	1.76	1.73	1.97	30	1.2
9 a.m.	1.77	1.66	1.94	32	2.0
10 a.m.	1.69	1.58	1.90	33	3.2
11 a.m.	1.52	1.45	1.81	31	2.7
12 noon	1.41	1.46	1.79	33	2.9
1 p.m.	1.50	1.48	1.77	35	4.1
2 p.m.	1.50	1.59	1.86	35	4.9
3 p.m.	1.70	1.55	1.89	30	5.0
4 p.m.	1.55	1.48	1.86	33	3.4
5 p.m.	1.68	1.70	1.86	30	4.2
6 p.m.	1.80	1.75	1.91	27	3.1
May 2					
6 a.m.	2.00	1.90	2.16	25	
7 a.m.	1.92	1.79	2.06	26	0.7
8 a.m.	2.01	1.91	2.29	29	(a)
9 a.m.	1.89	1.86	2.08	27	(a)
10 a.m.	1.89	1.78	2.05	29	(a)
11 a.m.	1.73	1.66	1.95	30	0.8
12 noon	1.66	1.58	1.94	33	2.0
1 p.m.	1.62	1.46	1.93	34	3.3
2 p.m.	1.59	1.49	1.99	34	4.1
3 p.m.	1.68	1.44	1.99	35	4.4
4 p.m.	1.62	1.51	1.99	35	4.0
5 p.m.	1.58	1.43	2.01	32	4.0
6 p.m.	1.66	1.57	2.03	27	3.1

a Rainfall during these hours.

TABLE 2—*Continued*

Time of Observation	Ave. Apparent Pinna Width (10 Pinnae on Each Plant)			Temperature	Evaporating Power of the Air (White Spherical Atmometer)
	Plant A	Plant B	Plant C		
	cm.	*cm.*	*cm.*	*deg. C.*	*cc. per hr. for preceding hour*
May 3					
6 a.m.	2.07	2.03	2.18	23	
7 a.m.	1.93	1.86	2.12	27	0.7
8 a.m.	1.78	1.67	2.06	28	1.2
9 a.m.	1.75	1.57	1.98	30	1.1
10 a.m.	1.59	1.49	1.92	32	1.9
11 a.m.	1.58	1.51	2.00	32	3.0
12 noon	1.57	1.42	1.89	35	3.4
1 p.m.	1.55	1.42	1.94	36	4.6
2 p.m.	1.59	1.43	2.00	33	3.8
3 p.m.	1.69	1.45	2.06	31	4.0
4 p.m.	1.63	1.40	1.90	31	2.3
5 p.m.	1.74	1.48	1.93	31	2.1
6 p.m.	1.82	1.59	2.03	30	1.5
May 4					
6 a.m.	2.02	1.90	2.06	24	
7 a.m.	1.74	1.75	2.02	25	0.9
8 a.m.	1.73	1.66	1.98	30	0.4
9 a.m.	1.66	1.50	1.99	29	2.1
10 a.m.	1.69	1.48	1.97	33	2.0
11 a.m.	1.66	1.47	1.97	34	3.5
12 noon	1.55	1.47	1.97	35	4.1
1 p.m.	1.52	1.35	1.91	36	6.9
2 p.m.	1.48	1.58	1.87	34	3.3
3 p.m.	1.62	1.62	1.76	33	3.3
4 p.m.	1.60	1.46	1.85	31	4.4
5 p.m.	1.68	1.50	1.89	31	4.1
6 p.m.	1.73	1.58	1.96	30	3.5
May 6					
6 a.m.	2.02	1.98	2.17	24	
7 a.m.	1.90	1.77	1.96	28	0.7
8 a.m.	1.70	1.60	1.96	28	1.4
9 a.m.	1.71	1.51	1.88	30	2.0
10 a.m.	1.67	1.50	1.81	32	(*b*)
11 a.m.	1.48	1.51	1.79	34	(*b*)
12 noon	1.52	1.39	1.79	32	3.8
1 p.m.	1.52	1.31	1.88	34	3.9
2 p.m.	1.50	1.33	1.92	35	4.0
3 p.m.	1.52	1.30	1.83	37	5.0
4 p.m.	1.48	1.33	1.94	35	4.6
5 p.m.	1.43	1.28	1.94	33	4.8
6 p.m.	1.55	1.35	2.03	32	1.7

b Accident prevented atmometer record.

area and the apparent pinna width. A smoothed graph, being a straight line, was then drawn for each of the five tests. The equations for the five rectilinear graphs have the general form, $y = Kx + L$, in which y represents the water content in grams per 100 sq. cm. of area (one side), x represents the apparent pinna width in centimeters, K is the slope constant of the graph, and L is another constant representing the value that y would have if the two pinna wings were in contact (the angle between them being then

zero), assuming that the rectilinear relation shown by the graph in question
were to hold at this stage of wilting or closing of the hinges.   The values
of K and L for each of the five equations are given in column 1 of table 1,
and are also brought together below:

Test No.	K	L
1	.3191	2.2272
2	.2825	1.6262
3	.2628	1.6338
4	.3457	2.1740
5	.1718	1.6021

After these equation constants had been derived for each test, the water-
content value was calculated, by means of the constants for the test in
question, for each apparent-width value given in table 1, and the "cal-
culated" water-content values are shown in column 5 of the table.   The
close agreement between the corresponding values of columns 4 and 5 shows
how nearly rectilinear the relation between water content and apparent
pinna width actually was for these tests.   The disagreements are generally
insignificant, and it seems safe to conclude that the linear equation form
represents a true relation for these pinna samples.   While there are con-
siderable differences between the values for K and between those for L
in the five tests (these differences being perhaps due to differences in
physiological state between the several lots of pinna samples, which were
selected at random), it may be stated that, in a general way, the values of
the two constants of proportionality for this relation of coconut pinnae
may be considered as: K, 0.3; L, 2.0.   If this statement approximates the
general truth, then the water content (in grams) for 100 sq. cm. of leaf
surface (one side) is numerically about equal to 2 *plus* one third of the
apparent pinna width (in centimeters); $y = 2 + 0.3x$.

Referring again to the diagram of figure 1, the apparent pinna width-
which seems to be directly related to the foliar water content, as just
noted—is itself truly proportional to the sine of half of the angle of diver-
gence between the two pinna wings, the two wings being of like width,
practically constant after the pinna has ceased to increase in size.   This
half-angle deserves special attention, for it represents the degree of diver-
gence of either pinna wing from the position that this wing would have if
it were in contact with the other wing—when the pinna would be com-
pletely "closed."   As has been mentioned, each wing is provided with its
own hinge, where it joins the pinna midrib.   The half-angle here con-
sidered is clearly a measure of the turgidity conditions in the hinge cells,
although the half-angle does not entirely vanish when all turgidity disap-
pears, the wings not coming into complete contact even when the pinna is
strongly wilted.

Since the sine of the half-angle just considered is directly related to the
apparent pinna width, and since the foliar water content is similarly related
to this width, it follows that the water content is likewise related to the

sine in question.   Considering the half-angle as A (the angular divergence of one pinna wing from its vertical or central position, this being one half of the angle of divergence between the *two* wings), the relation between foliar water content and the magnitude of angle A is shown by the following general equation of proportionality:

$$y = M \text{ sine } A + L,$$

in which y and L have the meanings given above and M is a new slope constant.   The values of M for the five tests with excised pinna samples are shown below:

Test 1	Test 2	Test 3	Test 4	Test 5
1.1041	0.9775	0.8961	1.0786	0.5704

Generalizing in a very rough way, it may be said that M is about unity, and that the water content of these leaves (in grams per 100 sq. cm. of area, one side) is numerically about equal to the sine of the angle of single-wing divergence *plus 2.*

Pinnae still attached.   Opportunity was not presented for the testing of the quantitative relations between foliar water content and position of the pinna wings with pinnae still attached to trees in the open.   As table 2 shows, the records of hourly changes in apparent pinna width throughout the day are useful in forming a picture of the diurnal march of these changes and, presumably, of the turgor fluctuations in the hinge cells, upon which the position of the pinna wings depends.   The maximum distance between the edges of the pinna occurred, on each day except May 2, at 6 a.m., the time of the earliest test, thus indicating that the hinge cells were more completely saturated with water at this hour than at any other hour at which tests were made.   The occurrence of the maximum at 8 a.m. on May 2 is probably related to a fall of rain that occurred between 7 and 8 o'clock on that day.   By 7 a.m. on most days the pinna wings had already begun to droop, and the angle of divergence continued to decrease, hour by hour, reaching a minimum value at some time between 11 a.m. and 5 p.m., the minimum width usually occurring between 1 p.m. and 3.   If Copeland's (2) interpretation of this phenomenon and the indications suggested by the present tests with excised pinnae represent what happens, it may be supposed that the greatest incipient drying occurred usually between 1 p.m. and 3.   After reaching the minimum the pinnae began slowly to open, and by 6 p.m. they had usually expanded to about the condition shown for 7 a.m. or 8.   Since other tests, continued throughout the night, showed that the maximum apparent width was reached some time early in the morning, and that it had begun to decrease somewhat by 6 a.m., when the tests here reported were begun, it is suggested that the maximum water content of the hinge cells probably usually occurs during the hours of darkness, very early in the morning.   The observed fact that the growth rate

of coconut is usually higher in the night than during the day is apparently related to higher water content of the plant as a whole in the night—at least to greater turgidity in the enlarging parts.

A comparison of the hours of occurrence of the minimum expansion for the three sets of pinnae measured (three different plants) shows that there was no constant relationship between the three sets as to the time of greatest drooping of the wings, though the minimum for plant C usually occurred earlier in the day than did the minima for the other two plants. From this variation it again appears (as was suggested by the tests with excised pieces) that individual differences between plants or leaves may result in somewhat different responses in incipient drying and wilting. The temperature and evaporation data given in table 2 show that in these tests the maximum temperature occurred between 1 p.m. and 4, usually between 1 p.m. and 3; and that the maximum evaporation rates occurred between noon and 3 p.m., most frequently about 2 p.m. or 3. Minimum temperature is shown in all cases for 6 a.m., and the minimum evaporation rate is shown for each day (except during rainfall on May 2) as occurring between 7 a.m. and 8. Had night readings been taken, they would undoubtedly have shown lower rates of evaporation than any during the day. A comparison of the recorded fluctuations in temperature and evaporation with corresponding fluctuations in wing position shows that the minimum leaf width usually occurred within one or two hours of the occurrence of the maximum temperature and the maximum evaporating power of the air, but that there was no very constant relation between these variations. If pinna expansion depends upon the turgidity and water content of the hinge cells, it would not be expected that a simple relationship would exist between either temperature or evaporation and angular divergence, since these external conditions affect the water content of only indirectly effective cells, by influencing the rate of water loss from the leaves and that of water absorption by the roots.

The hourly variations in the wing position for these coconut leaves resemble similar variations that other workers have observed in water content and wilting for many other kinds of plants. Thus the minimum water content observed by Livingston and Brown (7) occurred usually within an hour or two of the time of highest evaporation rates, the minimum moisture content of the leaves of most of their plants occurring between 1 p.m. and 5. Lloyd (9) found that the water content of the leaves of *Fouquieria splendens* began to decrease at daybreak and reached a minimum some time between noon and 4 p.m.; after that time the water content increased until about 4 a.m. With the cotton plant Lloyd (10) found that the minimum water content of leaves was reached at about 2 p.m. Miller (11), studying maize, milo, and kafir, found that all three of the plants showed a decreased water content between 7 a.m. and 11; in one third of his observations on maize and milo and in one fifth of those on kafir, the

leaves showed a gain in their leaf water content between 11 a.m. and 1 p.m. And from 1 p.m. to 3 the leaves gained in water content in one half of his observations on maize and milo and in three fourths of those on kafir, while from 3 p.m. to 5 the leaves of kafir showed a gain in water in all observations.

In the case of *Cestrum nocturnum*, Brown and Trelease (1) found that young shoots wilted and actually decreased in length, instead of elongating, on dry days during the time they were exposed to direct sunlight; in the night such shoots elongated rapidly, but during the day they showed no elongation excepting after they had returned to their original length late in the afternoon. Absence of growth and actual shrinking were apparently connected with excessive transpiration, which caused the plants to lose water more rapidly than they absorbed it. The movements of coconut pinnae appear to be similar also to the shrinking of tree trunks observed by Kraus (5), of fruits observed by Darwin (4) and by Smith (15), and of leaves observed by Thoday (16). Thoday found that leaves may shrink in area as much as six percent. During periods of intense sunshine, the minimum area usually occurred at about noon, and alternating periods of cloudiness and sunshine during the middle of the day were accompanied by prompt increases and decreases, respectively, in leaf area. The reversible movements of coconut pinnae are apparently due to alterations in the moisture content of the thin-walled "hinge" cells that lie in a row at either side of the midrib, the "hinge" cells apparently changing readily in shape or size, or both, with even slight variations in their water content. But it is not to be expected that fluctuations in the average water content of the whole pinna would be accurately and promptly reflected in turgidity changes and in resulting movements of the hinge tissues. There may be a considerable *lag* between leaf movements and alterations in the general foliar moisture, and the hinge cells may be peculiarly sensitive to alteration in the relation between transpiration and water supply. The possible action of light or temperature as a stimulus, high rates of evaporation, or changes in carbohydrate or acid content of the hinge cells or of the foliar tissues, etc., may also affect the relationship between the hinge tissue and the rest of the pinna. The occurrence of saturation deficit in plant tissues follows periods during which transpiration rates have exceeded rates of absorption. The physiological importance of such deficits has been emphasized by Livingston and Hawkins (8), who point out the possibility that the critical value of the ratio of transpiration to absorption (indicating the tendency of the plant to have its moisture content reduced) at which growth or other vital activity may be definitely affected, may eventually become recognized as a physiological and ecological constant, by which some of the over-discussed "adaptations" of plants may be quantitatively stated, at least in an approximate way.

Livingston and Brown (7) have suggested that in the diurnal minimum in the water content of foliage leaves we may have a criterion of some im-

portance to scientific agriculture, at least for arid regions, since by this criterion it may be possible to determine, indirectly, the status of the water relations of the plant, and to foresee the need of increased soil moisture, long before the usual criterion of cessation of growth or actual wilting becomes manifest. The movements of coconut leaves considered in this paper suggest a possible use of such changes in leaf position in connection with practical agriculture. It seems very important to have easily determined quantitative methods by which the condition of a crop may be judged, as a basis for proper methods of cultivation. The most convenient general index of the health of the plant, according to Copeland (3), is the growth rate. Although such indices are very much needed, agronomy and plant physiology have furnished few that may be conveniently applied, mere general inspection usually having to serve as the basis for judging the condition of a crop. If changes in the pinna movement of coconut, or similar changes in the leaves of abaca and banana (which have been observed by the writer), represent changes in water content of the leaf tissues, measurements of these may prove to be of value in connection with the practice of irrigation; the degree of movement or its duration, the hour of greatest closing or of maximum expansion, or the range between maximum and minimum apparent width, may be of more value as a criterion for irrigation practice than mere observations on the appearance of the plant or of the soil. The yields of such plants as coconut, abaca, and banana might thus be increased considerably by a judicious use of irrigation, even in localities having apparently suitable, but not optimal, moisture conditions. It may even be possible to use plants exhibiting such leaf movements as indicators for the irrigation or cultivation of other kinds of crop plants whose leaves do not show reversible movements correlated with their moisture content.

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